FURTHER NOTES ON THE TAXONOMY AND BIOLOGY OF THE ANDRENINE BEES ASSOCIATED WITH OENOTHERA

(Hymenoptera: Andrenidae)

E. G. LINSLEY and J. W. MACSWAIN[1]

University of California, Berkeley

Since the publication of observations on the nesting habits and flower relationships of three superficially similar species of *Andrena* which were collecting pollen from *Oenothera dentata* var. *johnstonii* in Short Canyon, on the western edge of the Mojave Desert near Inyokern, Kern County, California (Linsley, MacSwain and Smith, 1955), an opportunity has been afforded to make observations on a similar complex of species in a Mojave Desert locality near Little Rock, Los Angeles County, California. Although the new observations are not as extensive as we would have liked, they are offered in the hope that some useful comparisons between the two ecological situations can be made. The dominant species at the Little Rock Site were *Andrena oenotherae* Timberlake and *A. flandersi* Timberlake, although *A. foxii* Cockerell and an undetermined species were present in smaller numbers.

TAXONOMIC NOTES

Onagrandrena Linsley and MacSwain, new subgenus

Medium sized species of *Andrena;* integument black, occasionally partially red or tinted with reddish or bluish; pubescence of females black or blackish-brown, of males predominantly white.

Female—Head with facial foveae wide, upper ends occupying most of distance between eye and lateral ocellus, lower ends narrower, scarcely extending below level of antennal insertions; process of labrum usually reflexed and emarginate at apex, occasionally with produced apex long and slender. Thorax with pleura coarsely punctured; propodeum usually coarsely sculptured, enclosure well-defined, finely rugulose to coarsely rugose; propodeal corbicula poorly developed; wings lightly tinted with black to heavily infuscated, anterior pair with three sub-marginal cells (rarely two), first recurrent nervure ending beyond middle of cell; legs with tibial scopa long, loose, hairs of outer face simple. Abdomen with terga distinctly punctate, posterior impressions without hair bands, frequently with impunctate margins.

Male—Head with facial quadrangle usually longer than wide; clypeus concolorous with integument of rest of face. Thorax with hairs of dorsum white or predominantly white (rarely bright reddish); wings lightly tinted

[1] The authors gratefully acknowledge the assistance of James M. Linsley in the collection of field samples of bees. Flower identifications, as for our earlier study, were provided by Helen K. Sharsmith of the University of California Herbarium.

with black to heavily infuscated, anterior pair with three sub-marginal cells (rarely two).

Type of subgenus: *Andrena oenotherae* Timberlake.

This subgenus is proposed for a group of closely related species which, in so far as is now known, collect pollen only from *Oenothera* or other onagraceous plants. *Onagrandrena* is closely related to *Diandrena*, and the latter subgenus was presumably derived from it or from a common ancestral stock. Both groups are limited to the area from the Rocky Mountains westward. Further, at least five species of *Diandrena*, including *A. (D.) sperryi* Cockerell, *A. (D.) cyanosoma* Cockerell and *A. (D.) parachalybea* Viereck, collect pollen from *Oenothera* or other Onagraceae (Timberlake, in litt.). Cockerell (1937) has previously called attention to the fact that the tibial scopa is composed entirely of long simple hairs in the species of *Diandrena* associated with onagraceous flowers.

Lanham (1949) assigned this group of species to *Melandrena* and we have followed him in our recent treatment (Linsley and MacSwain, 1955). However, the *Oenothera*-visiting species do not seem to us to be closely related to either the Old World *Andrena morio* Brullé, which Hedicke (1933) designated as the type of *Melandrena* Pérez (1890) or to the North American *Andrena nigra* Provancher, which Lanham also assigned to *Melandrena*. Both of these species have a compact tibial scopa and facial foveae which extend well below the antennal insertions. *A. (M.) morio* visits crucifers and filaree (Friese, 1926), as well as *Anchusa* and *Centaurea* (Schmiedeknect, 1930); related species visit *Salix*, *Taraxacum*, *Brassica*, and *Sisymbrium*. *A. nigra* collects pollen from *Phacelia* (Linsley and MacSwain, 1955).

In addition to the species mentioned below, the following should be assigned to *Onagrandrena: A. (O.) prima* Casad, *A. (O.) anograe* Cockerell, *A. (O.) blaisdelli* Cockerell, *A. (O.) rozeni* Linsley and MacSwain, *A. (O.) rubrotincta* Linsley, *A. (O.) linsleyi* Timberlake, *A. (O.) mojavensis* Linsley and MacSwain, *A. (O.) deserticola* Timberlake, *A. (O.) vanduzeei* Linsley, and *A. (O.) omninigra* Viereck.

Andrena (Onagrandrena) oenotherae Timberlake

As we have indicated previously, *A. (O.) oenotherae* as identified by us either is an unusually variable species or a complex of closely related forms which we have been unable to segregate. The

Little Rock specimens, like those from the population in Short Canyon, vary in size, in the length and shape of the process of the labrum, the sculpture of the enclosure of the propodeum, and the punctures and shininess of the mesoscutum. In typical examples of *oenotherae*, the apex of the labral process is distinctly longer than broad, narrowed near the base. Of 57 females from Little Rock assigned by us to this species, only 13 have this type of labral process. These individuals are also somewhat larger, ranging in wing length from 8.6–9.6 mm., as against a range of 8.1–9.1 mm. for the remainder. However the mean wing lengths differs only by 0.2 mm. (9.0:8.8 mm.). Since the longer process of the labrum is associated with individuals in the larger size range, it is possible that heterogony is involved. However, all of the variations mentioned run to *oenotherae* in our recent key to the species of the subgenus (Linsley and MacSwain, 1955).

Andrena (Onagrandrena) species

Two female specimens from the Little Rock locality have been set aside as probably representing an undescribed species. They are of the size and form of *A. (O.) flandersi* but differ in the narrow impunctate margin of the metasomal tergites.

Andrena (Onagrandrena) foxii Cockerell

Andrena foxii Cockerell (1898) was assigned by Lanham (1949) to the subgenus *Diandrena,* presumably because the wings have only two submarginal cells and the integument, although black, has a metallic bluish cast. The species actually exhibits a number of structural characters of both *Diandrena* and *Onagrandrena* and might well be regarded as an intermediate type. However, the aspect of both sexes is that of the latter subgenus and since its biological characteristics also suggest such a relationship, we prefer this subgeneric assignment.

Although we identify our specimens with some confidence with the females described by Cockerell, Cresson (1928) unfortunately selected the male, which was only briefly characterized by Cockerell, as the type. Therefore, our identification rests on the assumption that the sexes were correctly associated by Cockerell.

Andrena (Onagrandrena?) phenax Cockerell

A. phenax Cockerell (1898) could not be subgenerically assigned by Lanham (1949) on the basis of the original description. However, if *A. foxii* is accepted as an *Onagrandrena* with two submarginal cells, then it is probable that *A. phenax,* which

shares this and other characters, merits the same assignment. The type is from southern California. Notes made some years ago distinguish the females of these two species as follows:

— Mesoscutum slightly shining, surface tessellate, with large, coarse, irregularly placed punctures intermixed with smaller ones, varying from one to several puncture widths apart, pubescence sparse, moderately short; process of labrum with apex very narrowly rounded.....*phenax*

— Mesoscutum dull, surface tessellate, with very fine, indistinct punctures, pubescence long, erect, dense; process of labrum with apex emarginate, more or less bilobed.....*foxii*

ANDRENA (ONAGRANDRENA?) STICTIGASTRA Viereck

A. stictigastra Viereck (1916), described from southern California, was also placed by Lanham (1949) in a list of species of uncertain position. From a study of the original description it would appear that it might well belong to the group of *Oenothera* monoleges here assigned to *Onagrandrena.* Viereck describes the species as "black, covered throughout with black or blackish brown hairs," the propodeum with the "enclosure well defined, coarsely sculptured in addition to having at least five well-defined longitudinal carinae on each side of a median longitudinal carina," the wing membrane "with a uniform blackish brown tinge." Although these characters are strongly suggestive of affiliation with *Onagrandrena,* the combination of small size (9.5 mm.), "dark brownish hairs on the mesopleurae," the "dorsulum dullish, finely reticulated, coarsely punctured, the punctures from nearly adjoining to six puncture widths apart, the punctures mostly sparsely distributed," and other features indicate that it is probably different from any of the subsequently described species which are now placed in this subgenus.

BIOLOGICAL NOTES

HABITAT

The *Onagrandrena* site which provided the observations here recorded is one mile west of Little Rock, Los Angeles County, in the western part of the Mojave Desert just north of the San Gabriel Mountains. The site is relatively flat and extends along both sides of a wash which is crossed by State Highway 138, the main thoroughfare from Palmdale to Little Rock. The area covered by us was about one-half mile wide and about three-quarters of a mile long. In this section the soil is a coarse sand with some gravel on the surface and buried rocks and small boulders which became more numerous as the lower levels of the

bee burrows were excavated. At the time of our study (April 23–28, May 12–15, 1956) the sand was moist from immediately below the surface to a depth of at least two feet.

As in the Short Canyon *Onagrandrena* habitat described previously (Linsley, MacSwain and Smith, 1955) there were scattered plants of *Larrea glutinosa* (creosote bush) and *Yucca brevifolia* (Joshua tree), and a perennial composite, *Encelia farinosa,* was abundant in both places. However, the species of *Oenothera* were different in the two sites. The pollen source for *Onagrandrena* near Little Rock was *Oenothera contorta* var., which closely resembles the Short Canyon pollen source, *O. dentata* var. *johnstonii,* in growth form (mostly 1–4 inches high), flower color (yellow), and flower size (½–¾ inch in diameter). However, unlike *O. johnstonii* which opened before sunrise, *O. contorta* did not open until the sun reached the flowers and, if the temperature was cold, not until the plants had been in the sun for some time. This fact markedly influenced the period of activity of the bees. A second yellow-flowered species *(O. micrantha)* with smaller blossoms was also abundant but only once was a female of *Onagrandrena* seen to visit this plant and it was not clear that pollen was taken on that occasion. A species with large white flowers *(O. californica),* although common, was ignored by *Onagrandrena,* but a few honeybees were seen gathering pollen from it. A major difference in the floral environment of the two areas was the great abundance of *Coreopsis californica* in the Little Rock site. These exceeded the flowers of *Oenothera* in numbers by approximately ten to one, and provided a ready source of nectar for the species *Onagrandrena.* A large number of females were captured while taking nectar from this plant. *Oenothera contorta,* although apparently an adequate pollen source for *Onagrandrena,* does not appear to produce as much pollen as *O. johnstonii,* at least as judged by the number of visits required to obtain a pollen load and the size of the loads carried by the bees which were captured.

The weather at the Little Rock site was extremely variable during the few days devoted to this study. In the period of April 23 to 28 there were no clear, warm mornings without wind. From May 12 to May 15, the morning sky was clear but again there was a strong east wind on May 12 and 14. This wind, which blew from the snow-covered San Gabriel Mountains, was cold and had a

delaying effect upon the opening of the *Oenothera* flowers and the emergence and other activities of the bees.

ANDRENA (ONAGRANDRENA) OENOTHERAE Timberlake

A. (O.) oenotherae was the largest and most abundant species of *Onagrandrena* found at the Little Rock locality and 57 females were collected. Of these, 23 were gathering pollen from *Oenothera contorta* var., 31 were taking nectar from flowers of *Coreopsis californica* and three were trapped in wire cones placed over burrows. The larger size of the females which we identify as *A. oenotherae* permitted recognition of the species in the field. The following account of its activities is based upon these 51 females and a smaller number which eluded capture.

Females were found to exhibit three principal behavior patterns. First, and particularly on the colder mornings, they emerged from their burrows and remained motionless on the ground in the sunlight. In this position they were seldom seen until they flew off as they were approached (none of these were captured). Within a few minutes after their first appearance on the ground, individuals were found gathering pollen from *Oenothera* flowers. The earliest pollen collecting female was seen at 6:45 a.m. on May 14, and the latest at 9:29 a.m. on May 12. The maximum time during which females were captured while gathering pollen on a given day was from 6:45 to 8:52 a.m. on May 14. On the previous day, which was colder, pollen collecting individuals were seen from 7:14 to 8:51 a.m. As mentioned above, the flowers of *Oenothera contorta* do not appear to produce as large a quantity of pollen as those of *Oenothera dentata* var. *johnstonii*, and females of *oenotherae* not only worked more flowers to obtain a pollen load than was true in Short Canyon, but the completed loads appeared smaller. Furthermore, the large numbers of *Coreopsis* flowers growing intermixed with *Oenothera* interfered with pollen gathering, since the bees also approached them for purposes of identification. Under these conditions, *A. (M.) oenotherae* were easily collected, although a few escaped capture in strong gusts of wind.

About an hour after the appearance of the first pollen-gathering bees, females (without pollen) were observed taking nectar from the flowers of *Coreopsis*. This characterized bee activity for about an hour after the last pollen-collecting female was seen. Between April 24 and April 28, more bees were found taking nectar than

gathering pollen; between May 12 and 15, the reverse was true. However, nectar-gathering bees were the more active and difficult to capture.

Females of *A. (O.) oenotherae* became active about the flowers near Little Rock about an hour later than in Short Canyon and activity extended for a longer period into the day. This difference may reflect a conditioning effect resulting from the different diurnal flowering behaviour of the two principal species of *Oenothera* and perhaps also the adaptability of this widely distributed bee.

Three burrows of the atypical form of *A. oenotherae* were located on May 14 and, after the capture of the bees, were filled with plaster of Paris. Excavation of the casts proved difficult because of the gravel and rocks encountered. Fortunately, only minor variations in the burrows were associated with rocks and the three casts were very similar in shape. Each was excavated on

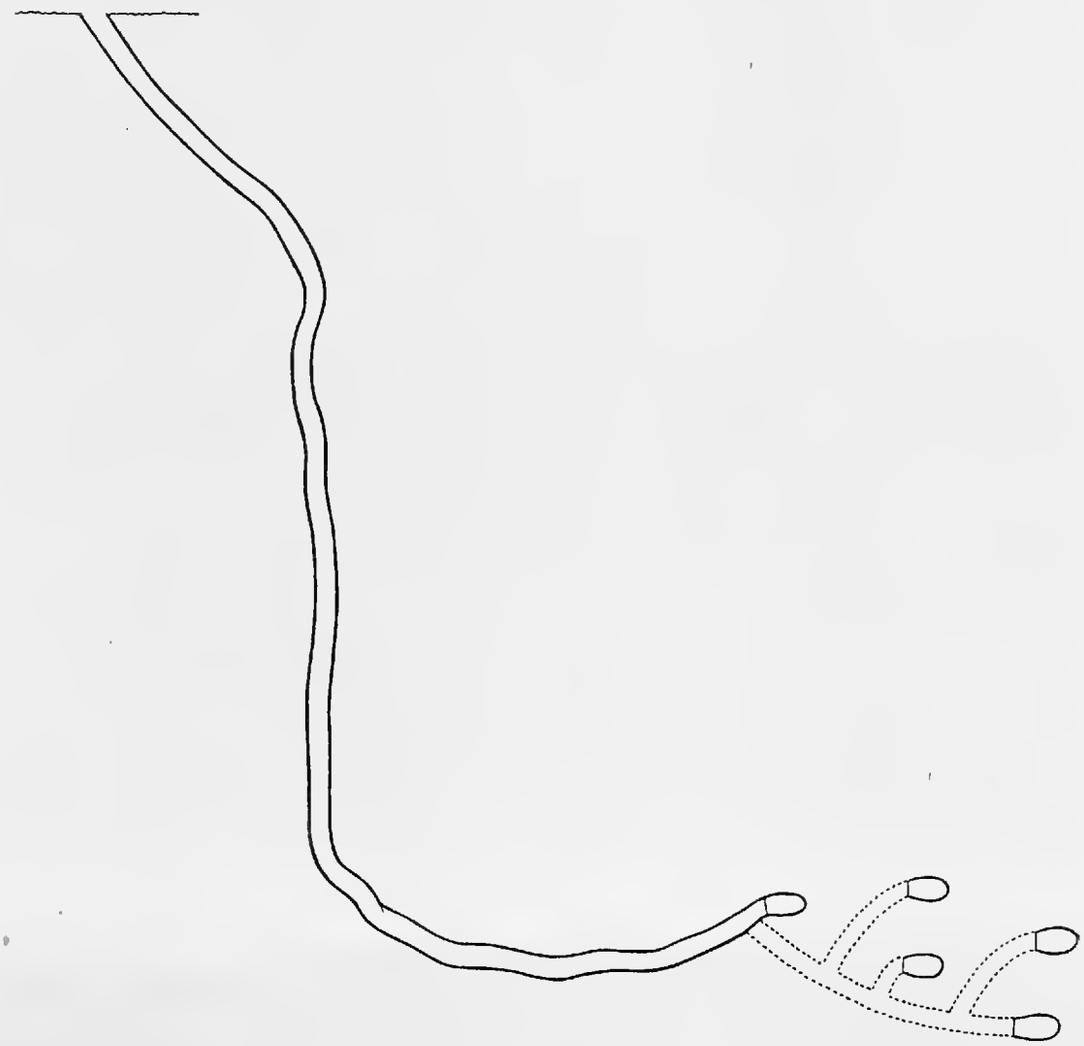

Fig. 1. Burrow diagram and cell arrangement in *Andrena (Onagrandrena) oenotherae* Timberlake, 1/5 natural size.

one side and measured *in situ* before removal. The burrows were about 7 mm. in diameter and slanted down from the surface of the ground to a depth of from 11 to 14 centimeters at an angle of about 45 degrees. From this point, they progressed vertically to a depth of 36 to 47 centimeters and then laterally for 12 to 20 centimeters where a horizontal open cell had been formed. Further excavations revealed a number of completed cells in the near vicinity, but since the tunnels connecting these with the lateral branch of the burrow had been plugged with sand, the exact relationship of these with the burrow can only be suggested (Figure 1). However, each cell was placed horizontally, measured about 14 mm. in length and 8 mm. in diameter, and contained a slightly flattened, spherical ball of *Oenothera* pollen. No larvae were found in the seven completed cells excavated and presumably only eggs were present.

A species of *Stylops* parasitic on *A. oenotherae* was also collected. Of three stylopized females (atypical form) taken on the flowers of *Coreopsis* on April 28, two contained a single female *Stylops* each, the third two female *Stylops*. First instar larvae were emerging from all of the female *Stylops* and continued to do so for several days after the bees had been killed in cyanide. The dorsal apex of the abdomen of each of the stylopized bees was covered with pollen grains of *Oenothera*.

ANDRENA (ONAGRANDRENA) FLANDERSI Timberlake

Seventeen females of *A. (O.) flandersi*, one of the smallest species now known in the subgenus, were collected at the Little Rock locality. Twelve of these were captured between April 25 and 27, four gathering pollen from *Oenothera contorta* var., eight taking nectar from flowers of *Coreopsis californica*. Five females found on May 12 and 13 were each taking *Oenothera* pollen. Our observations are limited to these 17 captured specimens since females of this species could not be distinguished in the field from those of *A. (O.) foxii* Cockerell or the undetermined species mentioned below. Although the number of individuals of *flandersi* collected was small, a comparison of the times of capture with those of *A. oenotherae* on the same days is of interest.

On April 25, after searching for bees from 5:00 until 6:00 a.m. without success, the area was left and then revisited at 8:30 a.m. At this time a number of bees were on the flowers of *Oenothera* and *Coreopsis* and the following four collections of

females of *oenotherae* and *flandersi* were made: from 8:30 to 8:50 a.m. (first collector) three *oenotherae* (1 with *Oenothera* pollen, 2 taking *Coreopsis* nectar) and three *flandersi* (all with pollen); from 8:30 to 9:15 a.m. (second collector), six *oenotherae* (all taking nectar) and one *flandersi* (taking nectar); from 8:50 to 9:20 a.m., two *oenotherae* (taking nectar) and two *flandersi* (1 with *Oenothera* pollen, 1 taking nectar); from 9:20 to 9:35 a.m., three females of *flandersi* (all taking nectar).

On April 26 at 6:10 a.m., the sky was overcast and the air was warm but by 7:36 a.m. it had turned quite cold, with intermittent showers. Only two bees were collected as follows: a female of *A. oenotherae* gathering *Oenothera* pollen at 7:12 a.m. and a female of *flandersi* inactivated on the ground at 8:19 a.m.

On April 27, at 6:10 a.m. it was clear and sunny but a cold wind was blowing from fresh snow deposited in the San Gabriel Mountains the previous day. Although the *Oenothera* flowers were fully opened by 7:45 a.m., the first bee was seen in flight at 9:11 a.m. Subsequently three bees were collected while taking nectar as follows at 9:16 a.m., a *flandersi* female, at 9:23 a.m., an *oenotherae* female, and at 9:26 a.m., a *flandersi* female. At 9:29 a.m., a female was seen in flight but no others were observed by 10:00 a.m. The following morning the area was visited between 7:00 and 8:30 and only *oenotherae* females were seen and collected. Three of these were stylopized, three were gathering pollen from *Oenothera* at 7:27, 8:01 and 8:09 a.m. and one was taking nectar from *Coreopsis* at 7:52.

The collections made in May suggest that *A. oenotherae* flies earlier in the day and may fly during weather conditions unsuitable for the smaller *A. flandersi*. On May 12, the area was visited at 8:30 a.m. and, although only a portion of the *Oenothera* flowers were open and a cold wind was blowing, six females of *A. oenotherae* and two of *flandersi* were collected. Five of the *oenotherae* were gathering pollen at 8:37, 8:42, 8:46, 8:52 and 9:29 a.m.; the sixth was caught at *Coreopsis* at 9:30 a.m. The two females of *flandersi* were collecting pollen when captured at 9:52 and 9:57 a.m. and other bees were seen later than this time. On May 13, there was almost no wind and bees were first observed at about 7:15 a.m. when only a portion of the flowers were open. These and the other bees seen and captured before 9:26 a.m. were recognized by their size to be females of *A. oenotherae*. Fourteen

of these (six with pollen at 7:15, 7:20, 7:47, 8:08, 8:44, 8:51 and eight with nectar at 8:09, 8:14, 8:18, 8:27, 8:34, 8:47, 9:04, 9:13) were collected. The next two bees encountered were females of *A. flandersi* taking pollen at 9:26 and 9:28 a.m. Another female with pollen was the last bee seen and collected at 10:07 a.m. In this last interval, however, two *oenotherae* were found taking nectar from *Coreopsis* at 9:20 and 9:59 a.m. On the morning of April 14, there was a strong, moderately cold east wind and although no females of *flandersi* were seen, eleven *oenotherae* were collected and a number of others seen. Seven of these bees, including the first at 6:45 a.m. and the last at 8:52 a.m., were gathering pollen, three were taken from *Coreopsis* and one as it emerged from its burrow at 7:05 a.m.

Several small burrows with vertical entrances were discovered too late to capture and identify their occupants or to investigate their structure. It is likely that they were the burrows of *A. flandersi* or of one of the other two small species known to occur in the area.

Although no males of *flandersi* were taken at Little Rock, two males and one female were collected at the Short Canyon site on April 12, 1954 (Linsley, MacSwain and Smith, 1955).

ANDRENA (ONAGRANDRENA) FOXII Cockerell

A. (O.) foxii is the only species of *Onagrandrena* from Little Rock of which males were collected. One of these was captured between 8:50 and 9:20 a.m. on April 25, the other at 7:11 a.m. on April 26. On April 28, a female was collected at 7:28 a.m. while gathering pollen from *Oenothera contorta* var., another while taking nectar from *Coreopsis californica* at 7:45 a.m. Although definite conclusions cannot be drawn from this sample, it should be noted that on April 28 the first female of *A. oenotherae* gathering pollen was collected at 7:27 a.m., the first individual taking nectar from *Coreopsis* was taken at 7:52 a.m. This suggests that *A. foxii*, unlike *flandersi* which appears later in the morning, may have a diurnal pattern of activity like *A. oenotherae*. However, the presence of the two males is puzzling since, in general, the species of *Onagrandrena* which appear latest in the season usually visit flowers latest in the day. It is possible that males of this species are long lived (the wings of both males are frayed), a characteristic that we have also observed in several species of the subgenus *Diandrena*. It should also be pointed out that in *Dian-*

drena, as in *Onagrandrena*, it is not uncommon to find a number of species collecting pollen from the same species of plant in the same locality (e.g., the complex of species associated with *Ranunculus*).

ANDRENA (ONAGRANDRENA) SPECIES

Two females of this species were collected on the flowers of *Coreopsis californica* on April 25. One was taken between 8:30 and 8:50 a.m., the other between 8:30 and 9:15 a.m. Although neither had pollen grains of *Oenothera* it is almost certain that this species also collects pollen from this source.

LITERATURE CITED

COCKERELL, T. D. A.

1898. On some panurgine and other bees. Trans. Amer. Ent. Soc., 25:185–198.

1937. Bees collected in Arizona and California in the spring of 1937. Amer. Museum Novitates, 948:1–15.

CRESSON, E. T.

1928. The types of Hymenoptera in the Academy of Natural Sciences of Philadelphia other than those of Ezra T. Cresson. Memoirs Amer. Ent. Soc., 5:1–90.

FRIESE, H.

1926. Die Insekten Mitteleuropas insbesondere Deutschlands. Band I. Hymenoptera, 1:1–192.

HEDICKE, H.

1933. Beiträge zur Systematik der Gattung *Andrena*. Mitt. Zool. Mus. Berlin, 19:199–220.

LANHAM, U. N.

1949. A subgeneric classification of the New World bees of the genus *Andrena*. Univ. Calif. Pub., Ent., 8(5):183–238.

LINSLEY, E. G. AND J. W. MACSWAIN

1955. The North American andrenine bees of the subgenus *Melandrena* with descriptions of new species. Pan-Pacific Ent., 31(4):163–172.

LINSLEY, E. G., J. W. MACSWAIN AND R. F. SMITH

1955. Observations on the nesting habits and flower relationships of some species of *Melandrena*. Pan-Pacific Ent., 31(4):173–185.

PEREZ, J.

1890. Catalogue des Mellifères du sud-ouest. Act. Soc. Linn. Bordeaux, 44:133–200.

SCMIEDEKNECHT, O.

1930. Die Hymenopteren Nord und Mitteleuropas. Fischer (Jena). 2 ed. vii + 1062 pp.

VIERECK, H. L.

1916. New species of North American bees of the genus *Andrena* from west of the 100th Meridian contained in the collections of the Academy of Natural Sciences of Philadelphia. Proc. Acad. Nat. Sci. Phila., 68:550–608.